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REINSTATEMENT OF THE FISSURELLID SUBFAMILY HEMITOMINAE, WITH THE DESCRIPTION OF NEW GENERA, AND PROPOSED EVOLUTIONARY LINEAGE, BASED ON MORPHOLOGICAL CHARACTERS OF SHELL AND RADULA (GASTROPODA: VETIGASTROPODA)

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ABSTRACT

The fissurellid subfamily Hemitominae Kuroda, Habe & Oyama, 1971, has been synonymized under the subfamily Emarginulinae by recent authors. Here it is redefined and characterized by a shell with either a short slit and selenizone, or a small notch without selenizone, and a radula synapomorphy, in which the rachidian and adjacent lateral teeth are of nearly the same size, the central field partitioned by a "transverse ridge." A generic review treating nine genera, including three new genera, is provided.

Three new genera – ***Hemimarginula***, ***Octomarginula***, and ***Variegemarginula*** – are considered basal, differing from the Mesozoic stem genus *Emarginula* Lamarck, 1801, in lower profile and by the shorter slit and radula synapomorphy. The genus *Montfortula* Iredale, 1915, is also basal, having a selenizone and notch visible in anterior view. The earliest basal member of the hemitomine lineage is the extinct *Loxotoma* Fischer, 1885, which arose in the Late Jurassic. Derived genera are *Montfortia* Récluz, 1843; *Montfortista* Iredale, 1929; and *Hemitoma* Swainson, 1840, which lack the slit and selenizone but have a notch in anterior view. *Montfortulana* Habe, 1961, and *Clypidina* Gray, 1847, are further derived, with the transverse ridge replaced by clumped pustules.

Instead of progressing to a shell form with an excurrent foramen at the apex (as in the derived emarginuline genera *Puncturella* Lowe, 1827, and *Diodora* Gray, 1821), this lineage reduces the prominence of the slit and leads to an imperforate shell that resembles the shell of other limpet groups.

My concept of the Hemitominae differs from that of the recent molecular phylogeny of Fissurellidae (Aptikis et al., 2011), which was poorly resolved, principally because it sequenced species of four rather than nine genera here determined as Hemitominae.

Key words: Fissurellidae, Hemitominae, subfamily classification, phylogeny, radular morphology, shell morphology, fossil record.

INTRODUCTION

The family Fissurellidae is the least understood of the vetigastropod limpet groups. There have been only three attempts to treat all species, that of G. B. Sowerby II (1862), which was continued by A. Adams (1863), that of Pilsbry (1890), who copied original descriptions and illustrations, and that of Thiele (1917), who also provided copies of the early illustrations. Most subsequent work has been done by authors of faunistic accounts, who have managed to determine local species (e.g., Wilson, 1993; Higo et al., 1999).

Previous efforts at subfamily-level classification are those of Pilsbry (1890): Emarginulinae, Fissurellinae, and Fissurellidinae; Thiele (1929): Emarginulinae, Fissurellinae; Wenz (1938): Emarginulinae, Diodorinae, Fissurellinae; Knight et al. (1960): Emarginulinae, Diodorinae, Fissurellinae; Christiaens (1977): Fissurellinae, Fissurellidinae, Emarginulinae, Scutinae; McLean (1984c): Emarginulinae, Fissurellinae; Christiaens (1991): Fissurellinae, Emarginulinae, Fissurellidinae, Hemitominae, Scutinae; McLean & Geiger (1998): Emarginulinae, Fissurellinae; Warén & Bouchet (2005): Fissurellinae, Emarginulinae (with other taxa as tribes under Emarginulinae).

The two-subfamily classification of Thiele, McLean, McLean & Geiger, and Warén &

Bouchet is based on a radula dichotomy that separates the Cenozoic-arising Fissurellinae from the Triassic-originating Emarginulinae. Further subdivisions of the Emarginulinae, whether as additional subfamilies or tribes, are here considered to be paraphyletic until the genera are better known. Genera that share features in common are recognized in my previous papers (McLean, 1984b, 1984c; McLean & Geiger, 1998) as "generic groups." Here, however, I attempt to show that in the Jurassic-appearing Hemitominae, there is a radula synapomorphy and synapomorphic shell morphology within the lineage, the recognition of which increases the number of monophyletic subfamilies to three.

The subfamily Hemitominae Kuroda, Habe, & Oyama, 1971, has had a checkered history of acceptance during the 40 years subsequent to its proposal. It was not recognized for the fissurellid text for *Fauna of Australia* by Hickman (1998). In the text for the Vetigastropoda of the *Working Classification of the Gastropoda* by Warén & Bouchet (2005), Hemitominae was synonymized without comment under the tribe Emarginulini of Emarginulinae.

Historical Chronology of Hemitominae

Thiele (1917, 1929) used only two genera – *Hemitoma* Swainson, 1840, and *Clypidina* Gray 1847 – for species treated here. He figured the radula for the type species of each genus, but gave no information on the radula of other species. Thiele (1917) also assigned 23 previously described species to *Hemitoma* and 17 described species to *Clypidina*. However, Thiele (1917) was prescient enough to recognize the affinity of many species of divergent shell morphology that are here assigned to additional genera based on shell morphology. Both genera were assigned by Thiele to the Emarginulinae.

The original proposal of Hemitominae (Kuroda, Habe & Oyama 1971: 10) is repeated here: "The shell conically elevated, cup-shaped, solid. Surface with distinct radial ribs and a short notch anteriorly. Radula has the rachidian tooth of ellipsoidal shape." This was lacking in detail for the radula, but at least mentioned that the notch is short.

Golikov & Starobogatov (1975: 185) overlooked Kuroda, Habe & Oyama, 1971, and separately proposed Hemitomidae as a full family among three families in the superfamily Fissurellacea, justified without a diagnosis in a footnote: "We find the differences from Emarginulidae and Fissurellidae important and our reasoning on the evolution of the Scutibranchia leads us to the conclusion that the Hemitomidae originated from other bellerophon-like ancestors." These remarks completely failed to characterize the group. In the same paper, Golikov & Starobogatov had speculated that fissurellids were descendants of Paleozoic bellerophontids, a concept further explored by McLean (1984a). However, the ancestral derivation of the Fissurellidae is still an open question, because the fossil record does not provide intermediate shell morphologies having the slit and selenizone.

Hickman (1980: 285) provided the first SEM illustrations of the radula of *Hemitoma octoradiata, Montfortula rugosa*, and *Clypidina notata*. "A more striking contrast is illustrated by the rachidian tooth within the superfamily Fissurellacea (the keyhole limpets and their allies). It is much reduced in development and characteristically asymmetrical in form. In the subfamily Fissurellinae, the asymmetrical cusp is narrow and rounded; in the subfamily Hemitominae, it is broader and denticulate and less obviously asymmetric; and in the subfamily Diodorinae, it is broad and simple. These morphologies are constant enough to be diagnostic at the subfamily level, although tooth proportions may vary considerably from one species to another or even among individuals from one population to another." These comments were incomplete as a diagnosis for Hemitominae, but Hickman did note that the rachidian tooth is less asymmetric than in Diodorinae and Fissurellinae.

Christiaens (1987, 1991) did not study radulae with SEM; he followed the example of Thiele (1917) and placed all species in *Hemitoma* or *Clypidina,* with the then-available taxa as subgenera; both genera were assigned by Christiaens (1987) to the Emarginulinae. However, he later (1991) reversed himself and recognized Hemitominae.

Herbert (1987: 1) remarked: "*Hemitoma* is here maintained within the Emarginulinae although several authors have elevated the taxon to subfamilial (Kuroda, Habe, & Oyama 1971; Hickman 1980) and even familial rank (Golikov & Starobogatov 1975). No reasons, however, have been given and such a high ranking at present seems unwarranted. The *Hemitoma – Clypidina* group appears to contain *Emarginula*-like forms adapted to a harsher intertidal and shallow water environment, largely in tropical to warm temperate regions." Herbert & Kilburn (1986) and Herbert (1987) did not examine hemitomine radulae with SEM. Herbert (1987: 1) noted that Hickman (1980) had illustrated "a pronounced 'transverse ridge' situated in the centre of the exposed face."

Herbert recognized *Hemitoma* and *Clypidina* (with subgenera), further stating that "… it is evident that a worldwide revision of the genus at subgeneric and specific level is required. The great variability of many species has given rise to a relatively large number of names, some of which will doubtless prove to be synonyms."

McLean & Geiger (1998) provided a phylogenetic analysis of selected genera of Emarginulinae, based on shell and radular characters. Their summary cladogram placed *Diodora* of the sometimes recognized Diodorinae within Emarginulinae. A review by McLean of hemitomine genera was anticipated to follow, which explains why the hemitomine genera were not mentioned by Geiger & McLean. This is therefore the culmination of that plan.

Initial work on the molecular phylogeny of Fissurellidae has just been published (Aktipis et al., 2011). Subfamilies recognized were Emarginulinae, Diodorinae, Fissurellinae, and Hemitominae (the latter of differing composition from that proposed here). A detailed critique of their work is given in the discussion section.

The objective here is to define additional genera and provide morphological details and comparisons for the shell and radula of all the recognized hemitomine genera, which will enable future efforts at phylogenetic analysis to be based on a more complete understanding of the genera and assigned species.

METHODS

For purposes of simplification and clarity, this effort is limited to analysis of characters of the shell and radula. Diagnostic morphological characters mentioned here for nine living genera and one fossil genus are summarized in Table 1. Terminology used here (e.g., evolutionary, lineage, basal, transitional, derived, etc.) is used in a traditional, non-restricted manner, without the implication that a complete phylogenetic analysis has been performed to produce a computer generated tree of my own.

Except for a few SEM illustrations provided by Hickman (1980, 1981), previous illustrations of hemitomine radulae have been line drawings (e.g., Thiele, 1917, 1929; Christiaens, 1987; Herbert, 1987). SEM illustrations for the radula of the type species or other species of the nine recognized genera are provided here. Prior to beginning my SEM work, a number of stained whole mount preparations of radulae were made. These whole mount preparations are also cited because they increase the number of examined specimens, and provide further evidence for the assumption that the radula is consistent in each genus. Voucher specimens of illustrated shells, or shells from which radulae were extracted for SEM preparations, are labeled in the LACM collection.

TABLE 1. Summary of diagnostic character states for radula and shell of hemitomine genera. Basal genera have a short slit and selenizone; derived genera have lost the slit and selenizone. Non-applicable character states are left blank. *Emarginula* is the outgroup (subfamily Emarginulinae). *Loxotoma* is here regarded as the oldest member of Hemitominae (Upper Jurassic of Europe).

Genus	Transverse ridge of radula	Shell profile	Primary ribs/ secondaries	Slit length	Selenizone	Notch in anterior view	Projecting anterior rib	Symmetry
Emarginula	lacking	varies	alternating	long	narrow			normal
Loxotoma	(fossil)	medium	alternating	short	broad			deflected
Hemimarginula	present	varies	irregular	short	narrow			normal
Octomarginula	present	low	eight	short	broader			normal
Variegemarginula	present	high	alternating	short	narrow			normal
Montfortula	present	medium	alternating		narrow	V-shaped		varies
Montfortia	present	high	irregular			V-shaped		normal
Montfortista	present	high	irregular			V-shaped	strong	varies
Hemitoma	present	low	eight			low		slight
Montfortulana	pustules	low	alternating			low		deflected
Clypidina	pustules	medium	alternating			lacking		normal

Shells of all genera treated here are illustrated for the exterior, interior and left side views. The notch of *Montfortula*, *Montfortia*, *Montfortista,* and *Hemitoma* best shows in a view of the anterior slope of the shell. Although this view is usually not provided in illustrations of limpets, it is provided here in order to show the extent of the notch (or its absence), and how its presence is not revealed in a standard exterior shell view.

Good illustrations for type species and other familiar species are also provided in the following regional identification manuals – Western Atlantic: Abbott (1974), De Jong & Coomans (1988); Eastern Pacific: McLean in Keen (1971); India: Subba Rao (2003); Japan: Higo et al. (1999), and for shell illustrations Sasaki in Okutani (2000); Philippines: Poppe (2008); Australia: Wilson (1993). Some species of the Indian Ocean were depicted by Herbert (1987); species of the Red Sea were illustrated by Christiaens (1989).

This effort is a generic level review; I am unable to verify the identifications of some previously illustrated species, but in the absence of a monographic treatment, I am assigning a few undetermined specimens or citing figures of other authors in order to demonstrate that all genera except for *Clypidina* are represented by additional species.

Museum abbreviations: LACM, Natural History Museum of Los Angeles County; SBMNH, Santa Barbara Museum of Natural History.

SYSTEMATICS

Subfamily Hemitominae
Kuroda, Habe & Oyama, 1971

Hemitominae Kuroda, Habe, & Oyama, 1971: 10. Type genus *Hemitoma* Swainson, 1840.

Hemitomidae Golikov & Starobogatov, 1975: 185. Not diagnosed; this is an objective synonym of Hemitominae Kuroda, Habe, & Oyama, 1971.

Revised Diagnosis

Body not greatly exceeding size of shell. Mature shell with nearly central apex, lateral profile low to elevated with slight posterior overhang of the apes. Sculpture of primary and secondary radial ribs. Anterior rib either split by short slit preceded by selenizone (= slit band) originating at apex; or, with slit only in juvenile stage, and anterior rib lacking selenizone, with strong to imperceptible notch at margin. Shell interior with narrow groove connecting notch or slit to apex. Muscle scar with hooks; area within muscle scar shaped like an inverted mushroom.

Rachidian tooth and three pairs of lateral teeth of nearly equal size; fourth pair of lateral teeth reduced; rachidian and lateral teeth with raised transverse ridge on inner face, or with similarly aligned, massive pustules on face of tooth shaft, lower part of shaft broader than upper; pluricuspid teeth with one or two main prongs, with smaller divisions on either side; marginal teeth like those of other fissurellids.

Shell Comparisons

Genera with the slit (the new genera ***Hemimarginula***, ***Octomarginula***, and ***Variegemarginula***) resemble the genus *Emarginula* in having a selenizone that precedes the slit, but the slit in all of these new genera is always much shorter than in the emarginuline genus *Emarginula,* and the lateral profile is usually lower than that of *Emarginula.* The established genus *Montfortula* has a narrow selenizone, but the slit does not show in dorsal view and is reduced to a notch visible in anterior view. In *Montfortia*, *Montfortista*, and *Hemitoma*, the selenizone is present in larval shells, but there is no selenizone in large shells, and a notch shows in anterior view. The notch is weak in *Montfortulana* and lacking in *Clypidina.* All genera, including those that lack the slit, have a low apex in central position or posterior to center; all have a groove on the shell interior that connects either the notch or slit to the shell apex. These shell characters are sufficiently reliable to establish the affinity of specimens known only from shells, enabling the assignment of both living and fossil specimens.

Shells of all hemitomine genera differ from emarginuline genera of low profile that have bodies larger than the shell (e.g., *Emarginella* Pilsbry, 1891*; Scutus* Montfort, 1810*; Tugali* Gray, 1843) in having the interior groove that connects the slit or notch to the apex.

Radula Comparisons

Herbert (1987: 1) introduced the term “transverse ridge,” for the mid-shaft partition that shows in the central field of the hemitomine radula, both in drawings and SEM illustrations (Figs. 1–10). This is a diagnostic, synapomorphic character that is unique in the Fissurellidae. In two genera (*Montfortulana* and *Clypidina*), the transverse ridge is replaced by a field of sharply projecting pustules (Figs. 11, 12); precursors to these pustules also show in the higher magnification images of ***Hemimarginula*** (Fig. 2) and ***Variegemarginula*** (Fig. 5), so these pustules are considered a derived character state for the transverse ridge in *Montfortulana and Clypidina*. These pustules for *Clypidina* were first illustrated by Hickman (1980: fig. 6a).

The hemitomine radula also differs from that of the Emarginulinae and that of the Fissurellinae in having the rachidian and lateral teeth of nearly equal size. The pluricuspid tooth is sufficiently large that it causes the radular asymmetry that characterizes both Emarginulinae and Fissurellinae, although the asymmetry is not as extreme as in either the Emarginulinae and Fissurellinae.

Thiele (1917, 1929) figured radula drawings of both *Hemitoma* (with the transverse ridge) and *Clypidina* (lacking the transverse ridge), a striking dichotomy, which could thereafter have served a purpose as long as the subgenera of subsequent authors were to be consistent with this distinction. However, the first available and useful taxon *Montfortula* was incorrectly assigned by Thiele himself (1929) to *Clypidina*, followed by Christiaens (1973, 1991), both of whom did not realize that *Montfortula* has a radula like that of *Hemitoma* rather than *Clypidina*.

Justification for Recognition of Hemitominae

The shell has a short slit or notch and the interior has a corresponding excurrent groove, unlike that of other fissurellids. The radula is synapomorphic for Hemitominae, having teeth of the central field (rachidian tooth plus lateral teeth) of similar size, with a prominent “transverse ridge” or pustules on the shaft, the teeth sufficiently cusped to have some role in feeding. This is unlike the emarginuline or fissurelline radula, in which the rachidian and laterals are not similar, do not have the transverse ridge, and are generally uncusped in species of large shell size.

Key to living hemitomine genera, with type species (*) and distribution

I. Radula with transverse ridge of central field
II. Radula with transverse ridge replaced by pustules

I. Radula with transverse ridge

A. With short slit and long selenizone within major anterior rib

Hemimarginula n. gen. Radial ribs markedly alternating in size [**dentigera*, Caribbean]. Other species in Caribbean and Indo-Pacific.

Octomarginula n. gen. Apex central, profile low, radial ribs of eight strong primary ribs [**ostheimerae*, Caribbean]. Other species in tropical eastern Pacific and Indian Ocean.

Variegemarginula n. gen. Apex recurved, radial ribs only slightly alternating in size [**variegata*, Indo-Pacific]. Other species are known from the Indo-Pacific.

B. With selenizone, but notch visible only in anterior view

Montfortula Iredale, 1915. Apex central, slightly recurved; radial ribs narrow, with low notch and narrow selenizone [**rugosa*, southeastern Australia]. Other species are known from the tropical Indo-Pacific.

C. Selenizone lacking, notch visible in anterior view

Montfortia Récluz, 1843. Apex raised and recurved, ends of shell raised; radial ribs with 3 enlarged anterior primary ribs [**australis*, Australia]. Other species in western Atlantic and eastern Pacific.

Montfortista Iredale, 1929. Apex raised and recurved, ends of shell raised; radial ribs with 3 enlarged anterior primary ribs, the central rib greatly extended anteriorly [**excentrica*, Indo-Pacific]. Other species in Indo-Pacific.

Hemitoma Swainson, 1840. Apex central, not recurved; radial ribs of eight enlarged primary ribs, secondaries reduced [**octoradiata*, Caribbean]. Another species in Indian Ocean.

II. Radula with reduced transverse ridge; notch lacking, with interior groove only

Montfortulana Habe, 1961. Apex posterior to center, radial ribs narrow, alternating primaries and secondaries, with faint notch and strong channel deflected to right [**sulcifera*, Indo-Pacific]. Other species are from the Indo-Pacific.

Clypidina Gray, 1847. Apex central, low in profile and not recurved; radial ribs narrow, black at crest, notch highly reduced [**notata*, Sri Lanka and India]. Monotypic.

REVIEW AND DESCRIPTIONS OF GENERA

I. Radula with transverse ridge

Group A – Genera with short slit and selenizone

Genus **Hemimarginula** n. gen.
(Figs. 1, 2, 13–18)

Type species: *Emarginula dentigera* Heilprin, 1889 (Fig. 13), previously misdetermined as *pumila* A. Adams, 1851 (see below). Other figures of type species: Abbott, 1974: fig. 41, as *pumila*; De Jong & Coomans, 1988: pl. 29, fig. 3, as *pumila*. Caribbean.

Shell (Figs. 13–18): Profile low to moderately elevated; primary radial rib count varies, each primary separated by secondary ribs of lesser size. Slit short, slit and selenizone within bifurcated anterior cord, flanked by two primary cords to make a raised anterior slope; color brown with lighter broad cords. Interior with a channel of selenizone width leading to apex.

Radula (Figs. 1, 2, *dentigera*): Rachidian of same width as laterals. Teeth of central field with transverse fold that forms a thickening above, with pustules below the ridge; pluricuspid with projecting prongs, with one short division on the inner side and two smaller divisions on outer side; large lateromarginal plate on outer side of pluricuspid.

Other Examined Whole Mount Preparations: *H. pileum*, LACM 177645; *H. pumila*, LACM 65-26.26.

Comparisons: *Hemimarginula* is usually characterized by the three anterior primary ribs that are broadly expanded, whereas in *Emarginula* the primary ribs remain narrow, with smaller secondary ribs added. Shells of *Emarginula* are usually white; whereas those of ***Hemimarginula*** may be brown with lighter colored primary cords.

Species: The three Caribbean species in Figures 13–15 have been confused by Farfante (1947) and by Abbott (1974). The first figure of the older name *pumila* A. Adams, 1851, provided by A. Adams & G. B. Sowerby II (1863: pl. 12, fig. 80), is oval in outline like that of Figure 14. Two subsequent names of Heilprin (1889) were confused by Abbott (1974). Figure 13 is here determined as a match for *dentigera* Heilprin, 1889, and Figure 15 as a match for *pileum* Heilprin, 1889, which has a higher profile, according to the original measurements.

Figure 17 shows an undetermined species of ***Hemimarginula*** from northwestern Madagascar, in which the apex is more anterior and the slit is a little shorter than that of the type species.

The Japanese species treated as *Emarginula biangulata* G. B. Sowerby III, 1901, by Sasaki in Okutani (2000: pl. 23, fig. 18) is clearly a member of *Hemimarginula* because of its very short slit and three stronger anterior ribs, the selenizone within the anterior rib; this is matched here by Figure 16.

Christiaens (1987) illustrated three species from the Red Sea that are here assigned to *Hemimarginula*: *subrugosa* Thiele, 1916 (figs. 68, 69); *modesta* H. Adams, 1872 (fig. 71), and *simpla* Christiaens, 1987 (fig. 43); his figures show the short slit, selenizone and the two adjacent anterior primary cords. Figure 18 here is a match for *subrugosa* of Christiaens, 1987.

Distribution and Occurrence: Recent members of the genus are known from the Caribbean and the Indo-Pacific from Japan to the Red Sea. This genus is characteristic of shallow water in tropical regions and occurs on under sides of rocks in the intertidal zone. *Hemimarginula* is a speciose genus of small-shelled species; many shells recovered from shell grit remain unidentified in the LACM collection.

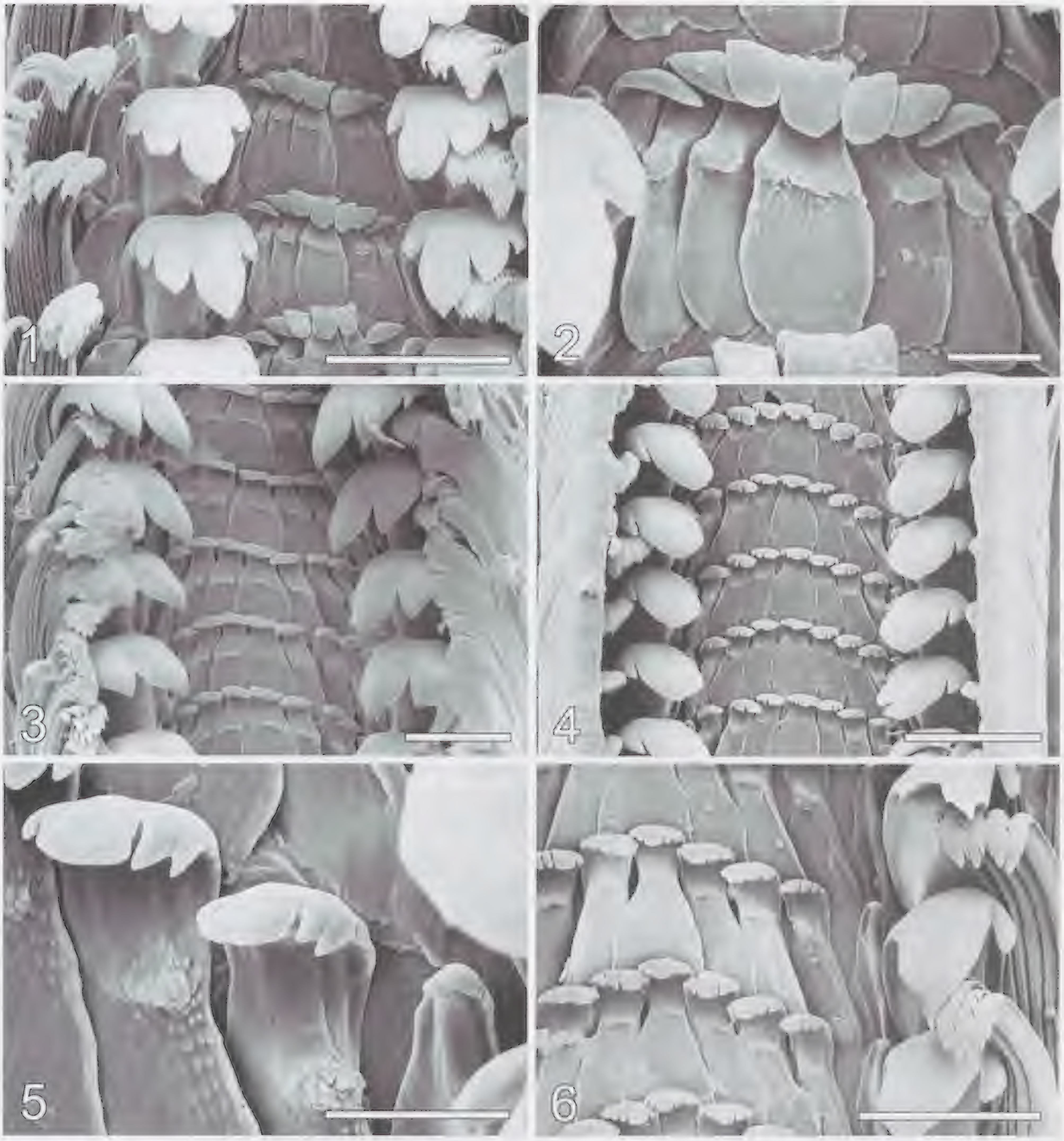
Fossil Record: The genus may be traced to the Pleistocene Caloosahatchee Formation of Florida with *Emarginula pilsbryi* Dall, 1892. Dall's species was also figured by Olsson & Harbison (1953: pl. 63, fig. 8).

Taxonomic History: Only Thiele (1917: 114) recognized the hemitomine affinity of the species *pumila* A. Adams, 1851, by placing it in *Hemitoma*. Farfante (1947: 108), did not cite Thiele (1917), but remarked that the type species was included by her in *Emarginula* "with some doubt." Christiaens (1987) was the only recent author to understand the affinity of this group; however, he did not propose a genus distinct from *Hemitoma*. *Hemimarginula* has an overall aspect more like that of *Hemitoma* than of *Emarginula*. Hence, the derivation of the name.

Genus **Octomarginula** n. gen.
(Figs. 3, 19–22)

Type species: *Emarginula ostheimerae* Abbott, 1958 (Figs. 19, 20) Caribbean. Other figure: De Jong & Coomans, 1988: pl. 29, fig. 7.

Shell (Figs. 19, 20, *ostheimerae*; 21, 22, *natlandi*): Profile of moderate height; apex central, not strongly projecting. Radial sculpture of eight primary ribs, secondary ribs of much lesser strength; each primary rib tending to be subdivided with size increase; concentric ribs

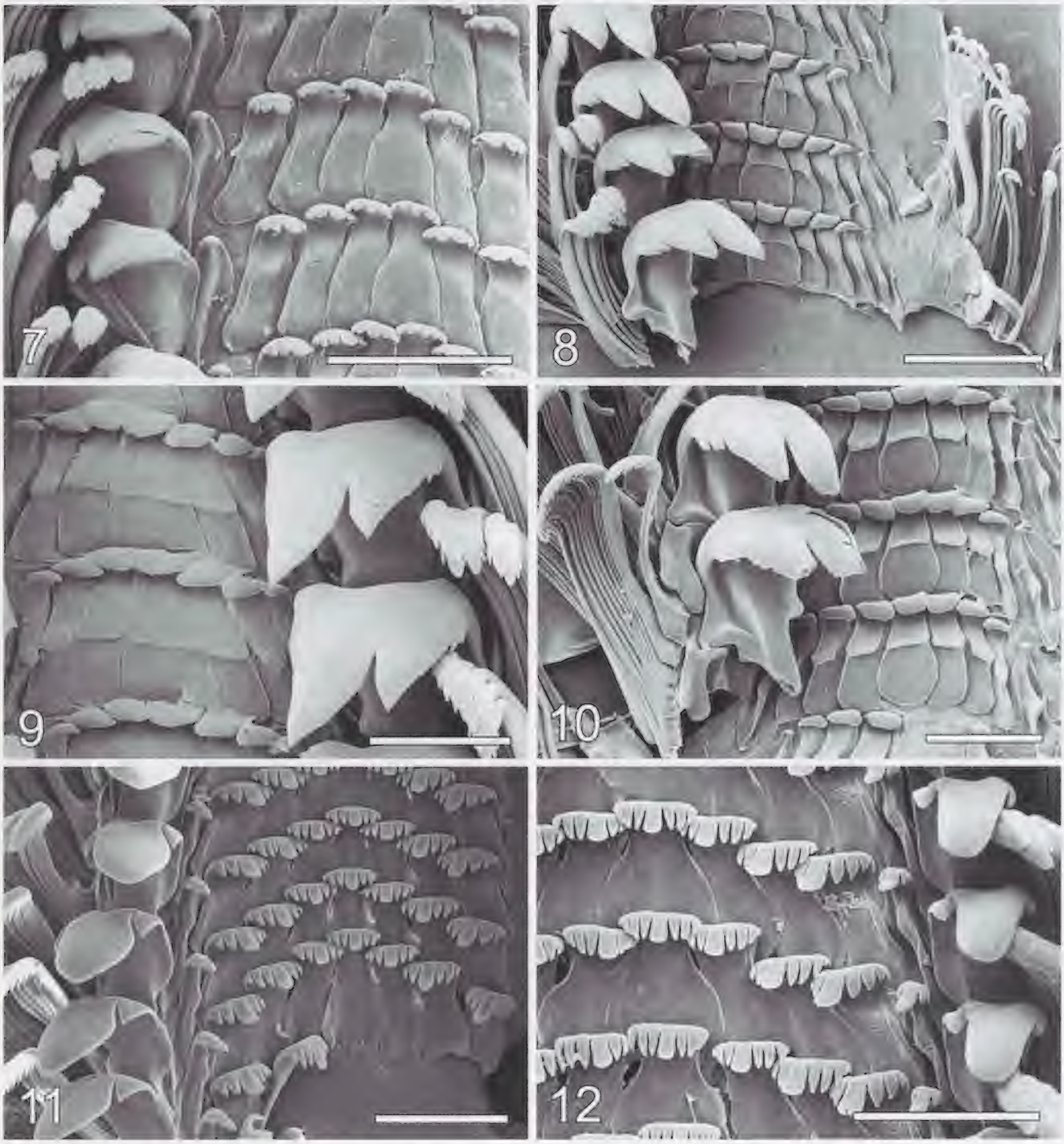


FIGS. 1–6. Radula morphology of hemitomine genera. FIG. 1: *Hemimarginula dentigera*, Portobelo, Caribbean Panama, 2 m. LACM 70-19.15. Scale bar = 100 µm; FIG. 2: Enlarged view of same. Scale bar = 20 µm; FIG. 3: *Octomarginula natlandi*, N side Santa Elena Peninsula, Ecuador, 9 m. LACM 66-114.26. Scale bar = 50 µm; FIG. 4: *Variegemarginula variegata*, S side Lizard Island, Queensland, Australia, intertidal. LACM 79-53.39 Scale bar = 100 µm; FIG. 5: Enlarged view of same. Scale bar = 20 µm; FIG. 6: *Montfortula rugosa*, Long Reef, Sydney, New South Wales, Australia, intertidal. LACM 79-58.7. Scale bar = 100 µm.

strong, broadly spaced. Short slit at margin, selenizone moderately broad, within anteriormost rib.

Radula (Fig. 3, *natlandi*): Rachidian of same width as laterals. Teeth of central field with transverse fold that forms a thickening above, pluricuspid with projecting prongs, with one division on the inner side and two on the outer side; large lateromarginal plate on outer side of pluricuspid.

Other Examined Whole Mount Preparations: *O. natlandi*, LACM 68-41.82.



FIGS. 7–12. Radula morphology of hemitomine genera, continued. FIG. 7: *Montfortula pulchra*, Guimeras Island, Iliola Province, Philippines, intertidal. LACM 74668. Scale bar = 100 µm; FIG. 8: *Montfortia emarginata*, Montego Bay, Jamaica, 1 m. LACM 65-26.24. Scale bar = 20 µm; FIG. 9: *Montfortia panhi*, Nusa Dua, Bali, Indonesia, intertidal. LACM 86-164.51. Scale bar = 100 µm; FIG. 10: *Hemitoma octoradiata*, Montego Bay, Jamaica, intertidal. LACM 65-26.25. Scale bar = 100 µm; FIG. 11: *Montfortulana* sp., Orofara, Mahina, Tahiti, French Polynesia, exposed intertidal basalt. SBMNH 83702. Scale bar = 100 µm; FIG. 12: *Clypidina notata,* Tangalla Bay, Sri Lanka, intertidal. LACM 83-5.1. Scale bar = 100 µm.

Comparisons: Shell sculpture of the major ribs is similar to that of *Hemitoma*, except that the anterior primary rib envelops a selenizone and there is a short notch in advance of the selenizone. The selenizone is broader than that of *Hemimarginula*.

Species: Western Atlantic, the type species *ostheimerae* Abbott, 1968. A large shell is shown in Figure 19; all previous illustrations have been of small specimens like that of Figure 20.

The Panamic species previously known as *Hemitoma natlandi* Durham, 1950 (Figs. 21–22; McLean in Keen, 1971: fig. 8), is here assigned to *Octomarginula* because it has a short slit and a selenizone comparable to that of the type species, and in having a central apex and a low number of primary ribs; small and large specimens are figured here.

The species *scutellata* Deshayes, 1863, from Reunion Island, Indian Ocean, as illustrated by Herbert (1987: figs. 1–5), is here assigned to *Octomarginula* because the illustrations clearly show a short slit and a somewhat broad selenizone.

The species from the Red Sea illustrated as *arabica* A. Adams, 1851, by Christiaens (1987: fig. 72) is here assigned to *Octomarginula*.

Distribution and Occurrence: Recent members of the genus are known from the Caribbean, the Panamic Province, and the Indian Ocean and Red Sea. Species of this genus occur in shallow water in the eastern Pacific and western Atlantic. It occurs on under sides of rocks in the intertidal zone; some specimens of *O. natlandi* are coralline encrusted and evidently live on exposed surfaces of rocks encrusted with coralline algae.

Fossil Record: *Octomarginula natlandi* was described as a Pleistocene species from the Gulf of California.

Taxonomic History: Previous authors have assigned the type species either to *Emarginula* (e.g., Abbott, 1958), or to a misunderstood concept of *Hemitoma* (e.g., Turner, 1959). The type species *O. ostheimerae* was incorrectly assigned to the synonymy of "*Hemitoma*" *emarginata*, by Turner (1959: 340), who did not examine or figure the holotype, which had been well illustrated by Abbott (1958).

Genus ***Variegemarginula*** n. gen.
(Figs. 4, 5, 23)

Type species: *Emarginula variegata* A. Adams, 1852 (Fig. 23). Indo-Pacific. Other figures: Sasaki in Okutani, 1990: pl. 22, fig. 2; Wilson, 1993: pl. 6, fig. 22).

Shell (Fig. 23, *variegata*): Profile elevated, apex recurved; gray and white or reddish, primary and secondary radial ribs of nearly similar size, ribs not scaly; often with two pairs of enlarged posterior ribs of lighter coloration; slit sharply defined, short and visible dorsally, selenizone narrow, formed between two half ribs.

Radula (Figs. 4, 5, *variegata*): Rachidian and laterals constricted below overhang, cutting edges with large median, subdivided by two prongs on the outer side and one on the inner side. Transverse ridge only slightly evident on rachidian, first three laterals with a "heel," on and below which there are projecting pustules. Fourth lateral narrow, with a medial ridge on face of shaft. Pluricuspid with broad, rounded main cusp, two deeply cut subdivision on outer side and one smaller one on inner side.

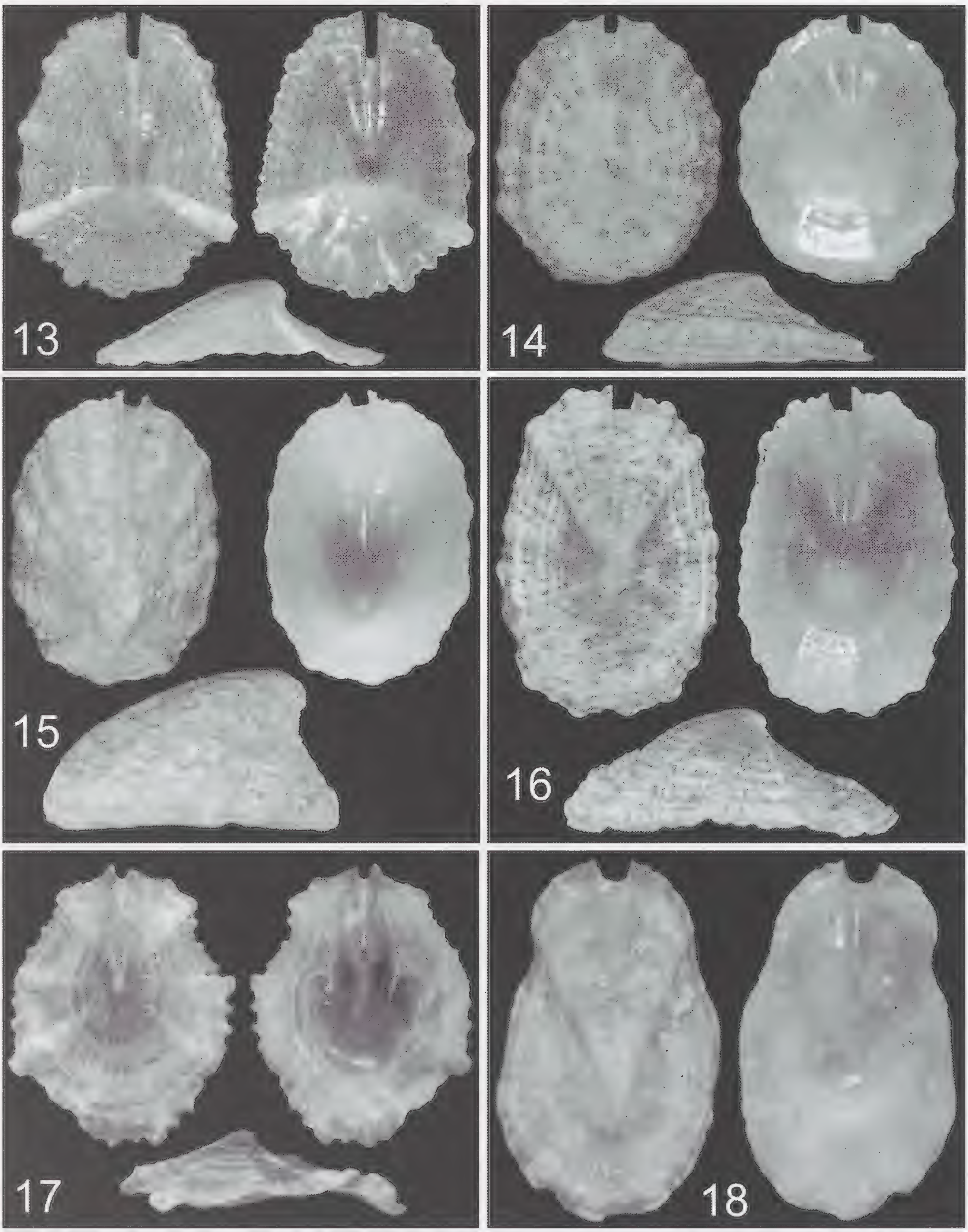
Other Examined Whole Mount Preparations: *V. variegata*, LACM 20783.

Comparisons: The shell of this genus differs from all species of true *Emarginula* in its variegated color pattern and in its short slit. This differs from the species of *Hemimarginula* in having uniformly fine radial ribs, not having the much broader primary ribs of that genus.

Species: *Variegemarginua variegata* has a high selenizone built by contributions from two half ribs. Two other species *punctata* A. Adams, 1852, and *foveolata fujitai* Habe, 1963, shown by Sasaki (in Okutani, 2000: pl. 22, figs. 1, 5) have similar sculpture and very short slits, so these species are provisionally assigned to the genus.

Distribution and Occurrence: The type species is common and widely represented in the LACM collection from Japan, the Philippines, and Queensland, Australia. Species occur in the Indo-Pacific only.

Fossil Record: Unknown.



FIGS. 13–18. Shells of **Hemimarginula** n. gen. FIG. 13: *H. dentigera*, Blauw Bay, W of Willemstad, Curacao, Netherlands Antilles, 30 m. LACM 74-28.6, 6.2 mm; FIG. 14: *H. pumila*, Montego Bay, Jamaica, shallow reef. LACM 65-26.26, 12 mm; FIG. 15: *H. pileum*, Big Pine Key, Florida, 1 m. LACM 177645, 6 mm; FIG. 16: *H. biangulata*. SE of Hedo Point, Okinawa, Japan, shell grit, 15 m, LACM 78-25.27, 7 mm; FIG. 17: *H.* sp., indet., Anpangorigina, Nosy Komba, Antseranana Province, off NW Madagascar, beach worn. LACM 89-56.3, 10.2 mm; FIG. 18: *H. modesta*, Southern Sinai Peninsula, Red Sea, Egypt, shell grit, 10–15 m. LACM 85-114.2, 5 mm.

Taxonomic History: Wilson (1993: 57, pl. 6, fig. 22) was the only previous author to have a clue about the affinity, by provisionally placing the type species in *Montfortula*.

Group B – With narrow selenizone, but notch visible only in anterior view

Genus *Montfortula* Iredale, 1915 (Figs. 6, 7, 24, 25)

Montfortula Iredale, 1915. Type species (original designation): *Emarginula rugosa* Quoy & Gaimard, 1834 (Fig. 22) Southeastern Australia. Other figures: Wilson, 1993: pl. 6, fig. 21.

Shell (Fig. 24, *rugosa*): Apex projecting, only slightly recurved, radial ribs numerous, alternating primaries and secondaries, notch visible only in frontal view. Short slit visible dorsally, under magnification it produces a selenizone in the middle of a primary rib that is slightly larger to accommodate the selenizone.

Radula (Fig. 6, *rugosa*): Rachidian and first three laterals with well marked transverse ridge at most constricted width of shaft; cusps with two to three deep cuts on either side; fourth lateral uncusped, with central ridge; pluricuspid with main overhang, concave on inner side, rounded on outer side; with lesser cusp on outer side; lateromarginal plate not exposed.

Previous SEM figures of radula *M. rugosa* – Hickman, 1980: pl. 1, figs. j, k; Hickman, 1981: figs. 8, 11, 12; Hickman, 1998: fig. L.

Other Examined Radula Preparations: Whole mounts, *M. rugosa*, LACM 68-81.3

Comparisons: *Montfortula* differs from the other basal genera *Hemimarginula*, *Octomarginula*, and *Variegemarginula* in not having a slit or notch visible in dorsal view. The narrow selenizone shows in dorsal view.

Species: The type species is common in southeastern Australia. This is the only species known in cool temperate waters; it has a lower profile than that of the tropical species currently assigned to the genus. There are no essential differences between the type species and other species (compare Figs. 6 and 7).

An unidentified species of *Montfortula* from the southern Japanese islands is figured here (Fig. 25); this species has the selenizone partially deflected to the right and it has larger and lighter colored posterior primary ribs than the type species. Note how similar large posterior ribs are also seen in certain species of *Hemimarginula* (Figs. 13, 17), and *Variegemarginula* (Fig. 23).

The Japanese species *Montfortula picta* (Dunker, 1860), as figured by Sasaki in Okutani (1990: pl. 25, fig. 41) is typical of tropical Indo-Pacifc species of higher profile; it is assigned to *Montfortula* because it has a short slit and selenizone within the anterior primary rib.

Also assigned is the species *brevirimata* Deshayes, 1862, *of* Herbert (1987: figs. 9–12, as *Clypidina*); it is assigned to *Montfortula* because it has a narrow selenizone within the large anterior rib.

Distribution and Occurrence: Southeastern Australia and tropical Indo-Pacific; *Montfortula* is not known in the Eastern Pacific and Western Atlantic.

Feeding: This species is a generalized grazer, feeding on fragments of microalgae and detritus. Analysis of stomach contents found large pieces of the algae *Ulva* and *Gracellaria*, as well as sponge spicules (Creese, 1978).

Taxonomic History: Thiele (1929: 34) placed *Montfortula* as a subgenus of *Clypidina*, which was subsequently followed by Christiaens (1977). However, the radula illustrations of Hickman (1980) established that the radula is comparable to that of *Hemitoma* rather than *Clypidina*.

Group C – Selenizone lacking, notch visible in anterior view

Genus *Montfortia* Récluz, 1843 (Figs. 8, 26)

Montfortia Récluz, 1843. Type species (subsequent designation, Iredale, 1915: *Emarginula australis* Quoy & Gaimard, 1834 [= *Emarginula subemarginata* Blainville, 1819]. Australia. Figure of type species: Wilson, 1993: pl. 6, fig. 34a–c.

Shell (Fig. 26, *emarginata*): Profile high, apex projecting, recurved, in some species deflected to right; sculpture coarsely clathrate, three strong anterior ribs; notch visible in frontal view in juvenile to mature stages, selenizone lacking in mature shell.

Radula (Fig. 8, *emarginata*): Rachidian and first two lateral teeth with strong transverse ridge; pluricuspid tooth with two large prongs and two weakly separated prongs on the outer edge.

Other Examined Radula Preparations: SEM for *Montfortia hermosa*, LACM 72-58; whole mount for *M. hermosa*, LACM 72-52.65; whole mount for *M. emarginata*, LACM 65-26.24.

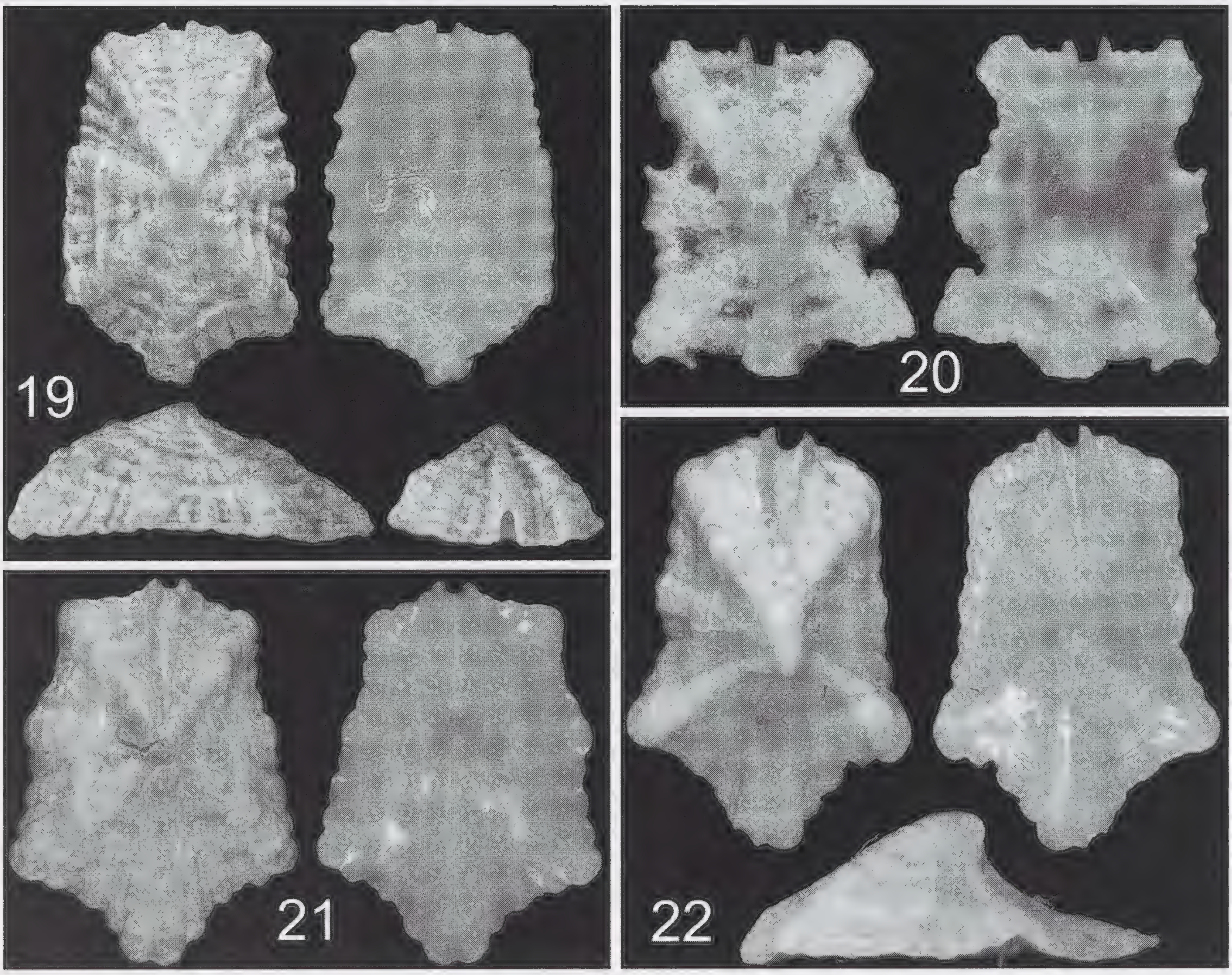
Comparisons: *Montfortia* is unlike other derived hemitomine genera in its three strong anterior ribs, the notch not visible in dorsal view of the shell. The anterior rib is not as projecting as it is in *Montfortista*. The radula of the species in the genera *Hemitoma* (Fig. 10) and *Montfortia* (Figs. 8, 9) is very similar.

Species: Australia (type species). Western Atlantic (Fig. 22, *emarginata* Blainville, 1825; Abbott, 1974, fig. 55). Eastern Pacific (*hermosa* Lowe, 1935; McLean in Keen, 1971: fig. 9).

Distribution and Occurrence: Southern Australia, Western Atlantic and Eastern Pacific, intertidal and shallow sublittoral zones.

Fossil Record: Early Pliocene of Jamaica. Illustrations of Woodring (1928: 40, figs. 6, 7) for his species *Hemitoma sclera* Woodring, 1928, are here considered indicative of the genus *Montfortia*, particularly because the ventral view shows the terminations of three strong anterior ribs.

Taxonomic History: Most recent authors have synonymized *Montfortia* and *Montfortista*, but



FIGS. 19–22. Shells of ***Octomarginula*** n. gen. FIG. 19: *O. ostheimerae*, large shell, reef off Doctors Cove, Montego Bay, Jamaica, 30 m. LACM 65-27.5, 12.2 mm; FIG. 20: *O. ostheimerae*, small shell, Western Dry Rocks, SW of Key West, Florida. LACM 87-104.1, 5.7 mm; FIG. 21: *O. natlandi*, large shell, Cuastocomate, Jalisco, Mexico. LACM 68-41.82, 14.3 mm; FIG. 22: *O. natlandi*, small shell, N side Santa Elena Peninsula, Ecuador, 9 m. LACM 66-114.26, 6.3 mm.

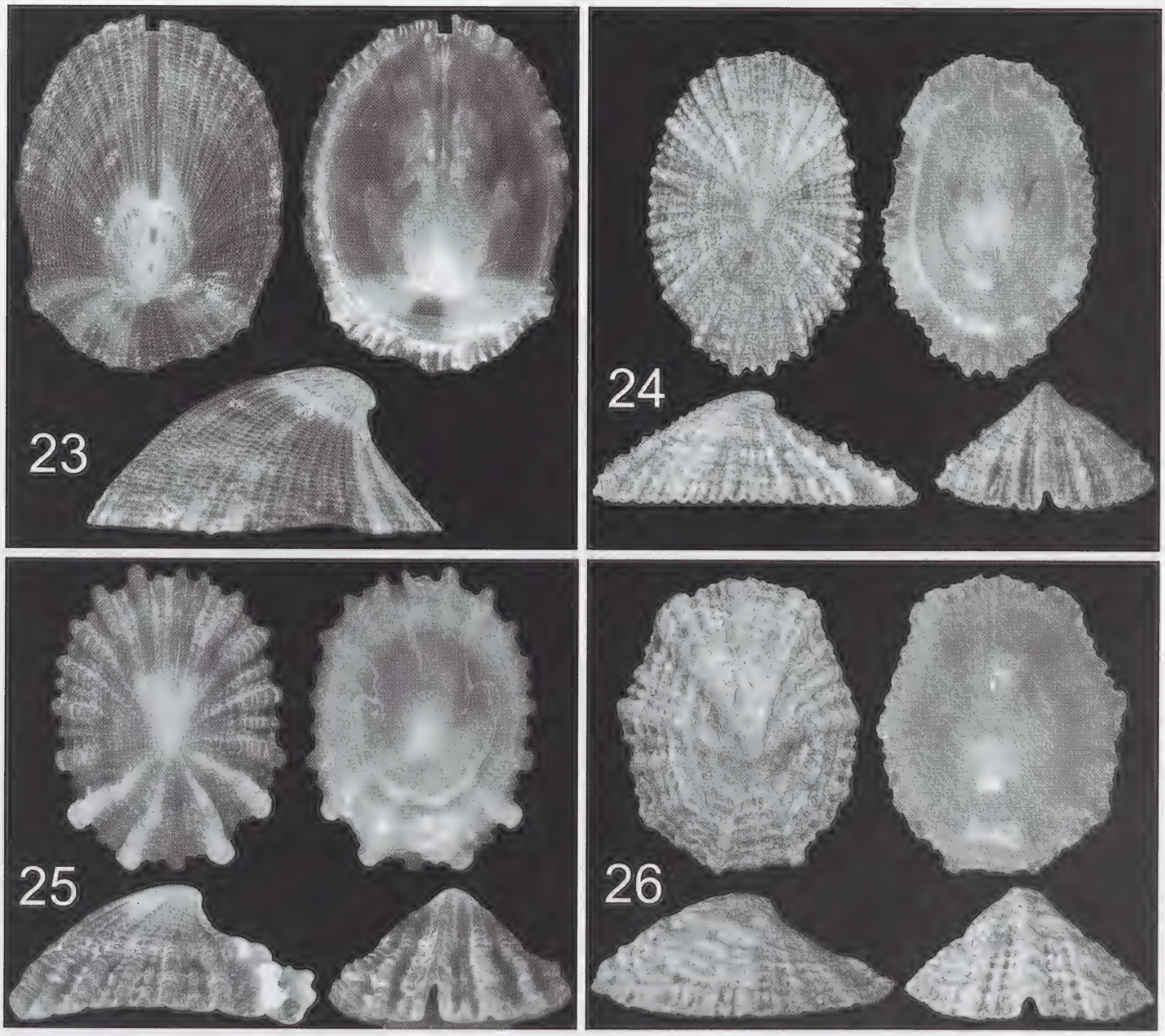
here they are recognized as distinct. Christiaens (1991) treated both taxa as synonyms of *Hemitoma*, but at least the radula for all three taxa is comparable.

Genus *Montfortista* Iredale, 1929
(Figs. 9, 27)

Siphonella Issel, 1869 (*non* Hagenow, 1851). Type species (monotypy): *Emarginula* (*Siphonella*) *arconatii* Issell, 1869 [= *Emarginula panhi* Quoy & Gaimard, 1834] (Fig. 27); Indo-Pacific. Other figure: Wilson, 1993: 57, text fig.

Montfortista Iredale, 1929. Type species (original designation): *Montfortia excentrica* Iredale, 1929. Northern Australia. Other figure: Wilson, 1993: 57, text fig.

Shell (Fig. 27, *panhi*): Profile high, apex projecting, recurved, in some species deflected to right; sculpture coarsely clathrate, three strong anterior ribs, the anterior rib strongly projecting beyond margin of shell; shells vary in position of juvenile stage with short slit; notch visible in frontal view in juvenile to mature stages, selenizone lacking in mature shell.



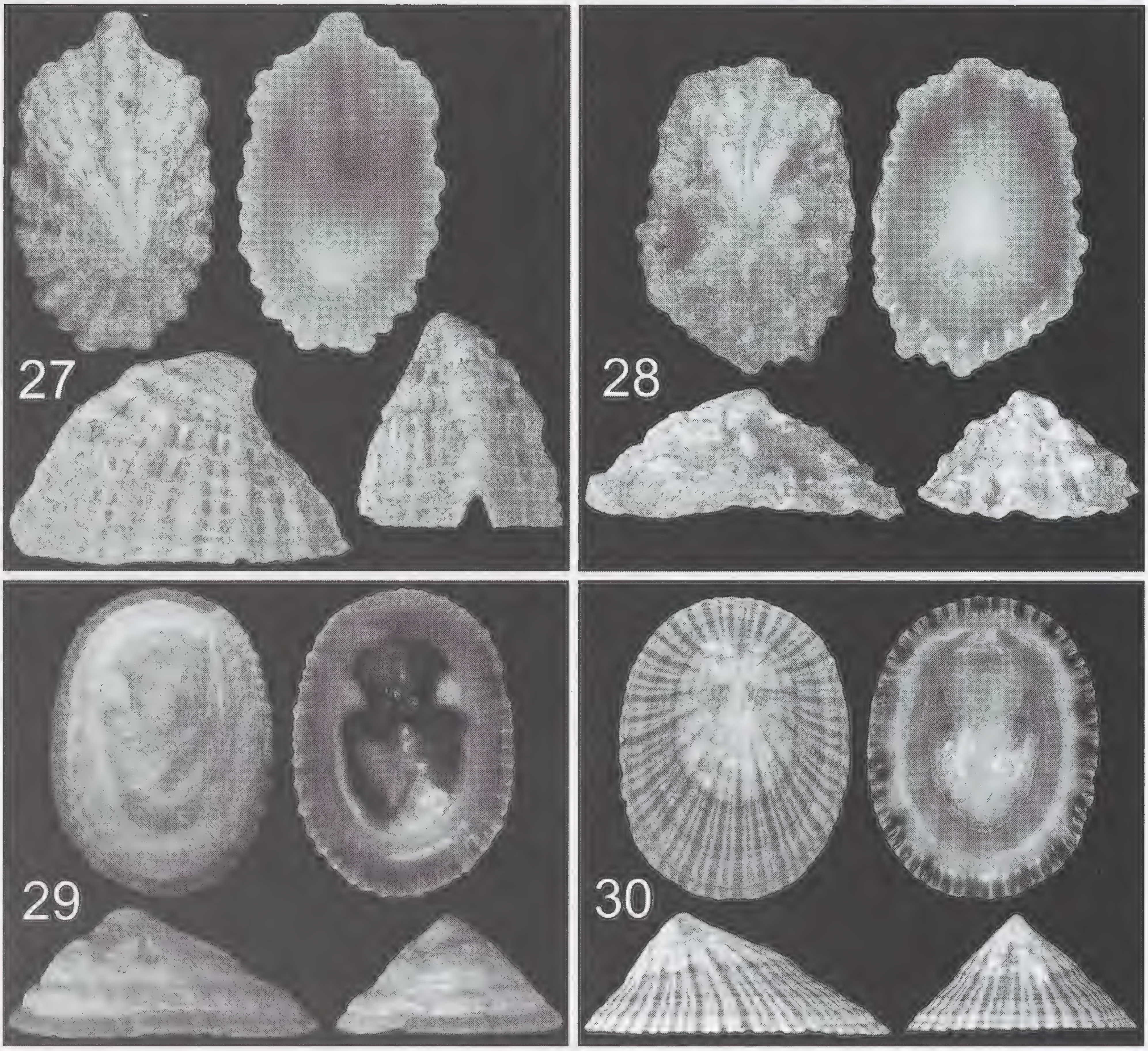
FIGS. 23–26. Shells of hemitomine genera, continued. FIG. 23: *Variegemarginula variegata*, Lizard Island, Queensland, Australia, intertidal. LACM 79-53.39, 8 mm; FIG. 24: *Montfortula rugosa*, Long Reef, Sydney, New South Wales, Australia, intertidal. LACM 79-58.7, 12 mm; FIG. 25: *Montfortula* sp., Oshima, Kagoshima Prefecture, Japan, LACM 25046, 11.5 mm; FIG. 26: *Montfortia emarginata*, Montego Bay, Jamaica, 1 m. LACM 65-26.24, 20.5 mm.

Radula (Fig. 9, *panhi*): Rachidian and laterals with well-marked transverse ridge; overhanging cusps continuous; pluricuspid with long, pointed inner cusp, and deeply separated outer cusp, with two very small accessory cusps.

Comparisons: *Montfortista* was intended for species that are strongly assymetrical, but the principal difference from *Montfortia* is that the anterior rib strongly projects beyond the anterior margin of the shell in dorsal view. Only by viewing the anterior slope of the shell is it possible to realize that there is a very strong notch.

Species: Australia (type species). Two Australian species that are assymetrical were assigned by Wilson (1993: 57): *panhi* (Quoy & Gaimard, 1934) and *excentrica* (Iredale, 1929; Wilson, 1994: 57 in text). For the Japanese species, Sasaki in Okutani (2000) included *panhi*, and *kirana* Habe, 1963, which have the strongly projecting anterior rib. For the Philippines, Poppe (2008) illustrated the species *kirana* Habe, 1963, and *panhi* Quoy & Gaimard, 1934.

One species illustrated by Sasaki in Okutani (2000: pl. 25, fig. 38) as *Montfortista oldhamiana* Nevill, 1869, has a different kind of



FIGS. 27–30. Shells of hemitomine genera, continued. FIG. 27: *Montfortista panhi*, Nusa Dua, Bali, Indonesia, intertidal. LACM 86-164.51, 15.2 mm; FIG. 28: *Hemitoma octoradiata*, Montego Bay, Jamaica, intertidal. LACM 65-26.25, 16.4 mm; FIG. 29: *Montfortulana* sp., Orofara, Mahina, Tahiti, French Polynesia, exposed intertidal basalt. D. L. Geiger 1587, 13.5 mm (exterior eroded); FIG. 30: *Clypidina notata*, Tangalla Bay, Sri Lanka, intertidal. LACM 83-5.1, 10 mm.

asymmetry in which there is a very strong rib on the posterior left, which places it outside the definitions of *Montfortia* and *Montfortista* as used here.

Distribution and Occurrence: Western Pacific, intertidal and shallow sublittoral zones.

Taxonomic History: Authors have generally regarded *Montfortista* as the same as *Montfortia*, but it is here distinguished from *Montfortia* in having a much more strongly projecting anterior rib.

Genus *Hemitoma* Swainson, 1840
(Figs. 10, 28)

Hemitoma Swainson, 1840. Type species (monotypy): *Patella tricostata* G. B. Sowerby I, 1823, *non* Gmelin, 1791 [= *Patella octoradiata* Gmelin, 1791] (Fig. 28). Caribbean. Other figure: Abbott, 1974: fig. 52.

Subemarginula Gray, 1847. Type species (monotypy): *Patella octoradiata* Gmelin, 1791.

Shell (Fig. 28, *octoradiata*): Selenizone lacking, shallow notch visible only in frontal view. Apex central, not recurved; eight strong primary ribs, with lesser secondary ribs between.

External Anatomy: The external morphology and the arrangement of the internal organs for *Hemitoma octoradiata* was illustrated by Odhner (1932: figs. 10, 11). The type species *octoradiata* is highly unusual for the Fissurellidae in having a narrow bright red edge to the foot and the mantle edge, which are green away from the edges.

Radula (Fig. 10, *octoradiata*): Rachidian and laterals with transverse ridge at middle position on shaft, upper region of shaft thicker than lower; overhanging edge not divided into finer cusps; pluricuspid with deep division, with two small cusps on outer edge; outer edge of pluricuspid articulating with lateromarginal plate.

Previous SEM figures of radula *H. octoradiata* – Hickman, 1981: fig. 7; Hickman, 1998: fig. K.

Other Examined Whole Mount Preparations: *H. octoradiata*, LACM 65-26.25.

Comparisons: This has the same number of primary ribs as in the new genus *Octomarginula*, but differs from that genus in not having the slit and selenizone. The shell differs from *Montfortia* and *Montfortista* in its eight ribs and non-projecting, non-recurved apex. The anterior view (Fig. 28) shows a notch that is less indented than that of *Montfortia* (Fig. 26) or *Montfortista* (Fig. 27).

Species: There are numerous synonyms for the type species cited by Turner (1959). A species from Mozambique determined by Herbert (1987: fig. 6) as *polygonalis* (A. Adams, 1852) agrees with *Hemitoma* in having the central apex and the count of primary ribs. The shell of the type species is always encrusted, as it lives exposed in intertidal zone.

Taxonomic History: This is the first named genus for the subfamily; it was used too broadly by Thiele (1917), and by subsequent authors. Most of Thiele's (1917) illustrations show species now assigned to other genera. Kilburn (1978: 478) keyed *Hemitoma* as having a selenizone forming a coarse ridge; such species with the selenizone are now assigned to *Montfortula* Iredale, 1915.

II. Radula with transverse ridge replaced by pustules, notch absent, with interior groove only

Genus *Montfortulana* Habe, 1961
(Figs. 11, 29)

Plagiorhytis Fischer (*non* Chaudoir, 1848), 1885. Type species (original designation): *Clypidina sulcifera* A. Adams, 1851. Locality unknown. Figure: Thiele, 1917: pl. 15, figs. 9, 10.

Montfortulana Habe, 1961. Type species (original designation): *Subemarginula* (*Plagiorhytis*) *eurythma* Dautzenberg, 1907. Lifou, Loyalty Islands. Figure: Thiele, 1917: pl. 14, figs. 10–12.

Shell (Fig. 29, species undetermined): Apex anterior of center, not recurved; radial ribs alternating with numerous primaries and smaller secondaries, anterior channel of inner surface deflected to right antero-lateral position, corresponding notch very weak.

Radula (Fig. 11, species undetermined): Transverse ridge condition obscured by dark lighting on shaft; cusps of rachidian and first three pairs of lateral teeth, deeply split on either side; fourth lateral narrow with narrow overhanging cusp; pluricuspid with broad, angular overhang, with one smaller cusp on outer side. Narrow lateromarginal plate between pluricuspid and inner marginals.

Comparisons: Differing from other hemitomine genera in having the notch and its interior groove running from the apex to the right antero-lateral corner. In having a reduced transverse ridge, the morphology of the rachidian and lateral teeth is most like that of *Clypidina*, differing in a narrower aspect of the tooth shafts.

Species: Two or three species, Indo-Pacific: *Clypidina sulcifera* A. Adams, 1851 ["hab. Unknown"]; *Subemarginula* (*Plagiorhytis*) *eurythma* Dautzenberg, 1907 [Lifou, Loyalty Islands]. The illustrated specimen from Tahiti (Fig. 29) is more elongate than the figures for the two species previously assigned, so it is likely to be an undescribed species.

Taxonomic History: The right anterior lateral position of the interior groove is well illustrated by Thiele (1917: pl. 15, fig. 10, *sulcifera* A. Adams, 1851, and pl. 14, fig. 12, *eurthyma* Dautzenberg, 1907), both of which were placed by Thiele in *Clypidina*. Christiaens (1991: 38) listed *Montfortulana* as a subgenus of *Clypidina*. Higo et al. (1999: 43) listed *Montfortulana* as a full genus of Emarginulinae. Unfortunately, Sasaki in Okutani, 2000, did not figure a Japanese species of *Montfortulana*.

Habe (1964: 4) provided an English translation of the original Japanese description: "The shell is roundly oval, conical, moderately elevated and rather solid. The apex is slightly anterior from the center. From the apex about 15 primary radial ribs run to the margin; there are sometimes secondary riblets between these main ribs. There is an internal groove running from the apex to the right antero-lateral corner, rather than to the anterior end as seen in the genus *Clypidina* Gray."

Genus *Clypidina* Gray, 1847
(Figs. 12, 30)

Clypidina Gray, 1847. Type species (monotypy): *Patella notata* Linnaeus, 1758 (Fig. 3) India and Sri Lanka. Other figure: Subba Rao, 2003: pl. 2, figs. 5, 6).

Shell (Fig. 28, *notata*): Large for subfamily, apex central, not recurved; radial ribs even, black at crests, short notch visible only in frontal view only in early juvenile shell, connecting to narrow anal groove leading to shell apex.

Radula (Fig. 11, *notata*): Rachidian and three pairs of laterals of similar size and morphology, with shaft broad at base; overhanging cusps deeply split; shafts of third pair of laterals with transverse thickening; fourth pair or laterals smaller; pluricuspid larger, with rounded main cusp and smaller side cusps. The radula of *Clypidina* is unlike other hemitomine genera (except for *Montfortulana*) in having the transverse ridge apparent only as a thickening with pustules on the third laterals.

Previous SEM figures of radula *Clypidina notata* – Hickman, 1980: fig. 6a.

External Anatomy: The anatomy of *Clypidina notata* was described and Illustrated by Odhner (1932: figs. 8, 9).

Comparisons: *Clypidina* is unique in not showing a notch in anterior view, although the shell interior has the channel that leads to the apex.

Species: The type species is known only from the Indian Ocean; LACM records are from Sri Lanka and Goa, India. It occurs in the exposed intertidal. This is probably a monotypic genus.

Taxonomic History: This genus has been used more broadly by early authors, including Thiele (1917: 126), particularly for a number of species later assigned to *Montfortula* Iredale, 1915, and *Montfortulana* Habe, 1961. As noted above, Christiaens (1973, 1991) incorrectly used *Montfortula* as a subgenus of *Clypidina*, contrary to the radula definition of Thiele, 1917, 1929).

DISCUSSION

Morphological Evidence in Support of Hemitominae

The hemitomine lineage of Fissurellidae is here diagnosed on shell and radular characters. The defining feature of the radula – the transverse ridge of the teeth of the central field – is a synapomorphy unknown in any other genera of fissurellids. The transverse ridge of the rachidian and laterals has previously been illustrated in the line drawings of Farfante (1947), Christiaens (1987), and Herbert (1987), but these drawings do not convey the three dimensional aspect revealed with SEM, that the upper part of the tooth is actually thickened at the juncture and projects to overlap the basal portion of the tooth. The transverse ridge has a derived state in the genera *Montfortulana* and *Clypidina*, in which it is expressed by projecting pustules.

On shell characters, the genera that retain the slit and selenizone in mature stages are regarded as the basal genera of Hemitominae, because an open slit and selenizone is plesiomorphic for *Emarginula*, which is the oldest known genus of Fissurellidae. The basal genera of Hemitominae differ from *Emarginula* in having a lower profile, a shorter slit, and more irregular primary and secondary radial ribs. The more derived genera of Hemitominae retain the groove, but have lost the slit and the selenizone, which has been replaced with a notch that shows in the anterior view of the shell, except for *Clypidina*, which lacks the notch.

The course of evolution of the two groups has differed. In the stem group Emarginulinae, the lineage with an open slit yields shell forms with the anterior margin closed, to enable the slit to become modified, first by becoming sealed at the margin as in *Rimula* Defrance, 1887, and enlarged as an excurrent foramen, in the process losing the selenizone in the mature shell, as in *Puncturella* Lowe, 1827. In the hemitomine lineage, the derived genera do not form excurrent holes in the shell; instead, the derived genera lose the selenizone in the mature stage, becoming more limpet-like, retaining only the small notch at anterior edge of the shell, which serves as the excurrent channel out of the mantle cavity.

It might be expected that the derived hemitomine genera would reduce the size of the paired ctenidia, considering that the direction of flow is reduced by the necessity for the current to exit the mantle cavity at the uppermost anterior edge of the shell, via the short slit or notch. However, the paired ctenidia illustrated by Odhner (1932), for type species of the genera *Clypidina* and *Hemitoma* are not smaller than those of other fissurellids. Both of these genera are in the derived group that lives exposed to wave energy in the intertidal, so it seems evident they are able to maintain the flow through the mantle cavity by living in a high energy environment.

Fossil Record of Hemitominae

The earliest occurrence of Hemitominae is here recognized in the genus *Loxotoma* Fischer, 1885, occurring from the Upper Jurassic to Eocene of Europe. The type species, *Loxotoma neocomiensis* (d'Orbigny, 1843), is a strikingly asymetrical species of the Neocomian Early Cretaceous of France, with a broad notch and selenizone on the right anterior-lateral margin, as figured by Knight et al. (1960: 228, fig. 141–7a, b). This genus agrees with my diagnosis of the subfamily in having a non-recurved central apex, with primary and secondary ribs alternating in strength, and a very short slit that is deflected to the right. The selenizone is broader than that of living genera, but it calls to mind the scooped short slit of the early stage of *Octomarginula* (Fig. 22).

Sohl (1992: 418, figs. 5.1–5.3) illustrated a specimen as "*Emarginula* sp.," from the Upper Cretaceous of Jamaica, which he left unnamed, because the low profile and lack of the posteriorly directed apex and broader selenizone than that of other Cretaceous species of *Emarginula* that he described in the same paper. The comparison was not made to *Loxotoma*, but it is now clear to me that Sohl's illustrated specimen is a *Loxotoma* with the slit not so deflected as in the figured type species of *Loxotoma*.

Sohl (1992) also noted that *Emarginula gabbi* Stewart (1927: 313, pl. 23, fig. 10), from the Campanian Late Cretaceous of California, "also has a depressed profile and strong radial sculpture, but the ribs are closer spaced and the selenizone is much narrower." Other species of similar profile are mentioned by Sohl (1992: 418). All of these species indicate that the basal forms of Hemitominae were broadly represented in the Mesozoic. The Mesozoic genera of Hemitominae are in need of further study, which is beyond the scope of this report.

Two of the living hemitomine genera have a fossil record in the Caribbean. These are the new genus ***Hemimarginula***, which has a fossil record in the Pliocene, as mentioned under that genus, and the genus *Montfortia* in the early Pliocene. Ladd (1966) illustrated a few species of hemitomine genera in his account of Cenozoic gastropods from island groups of the Western Pacific, nearly all of which were of Holocene age; he cited the then available literature by region.

Recurring Asymmetry of Hemitomine Genera

A rightward shift in the position of the selenizone is a recurring theme in the Jurassic to Cretaceous genus *Loxotoma*, one undetermined living species of *Montfortula* illustrated here (Fig. 25), and the living genus *Montfortulana* (Fig. 29). There are less pronounced indications of asymmetry in *Octomarginula natlandi* (Figs. 21, 22), *Montfortia emarginata* (Fig. 26), *Montfortista panhi* (Fig. 27), and *Hemitoma octoradiata* (Fig. 28). Similar patterns of asymmetry are unknown in living species of Emarginulinae and Fissurellinae.

Shell and Radula Evolution of Subfamily Fissurellinae

All genera of the subfamily Fissurellinae have an apical foramen and are therefore not derived from the stem genus *Emarginula*, but must be derived from a foramen-bearing group. The candidate group would be unlike *Diodora*, not having a truncate callus bordering the inner edge of the foramen, and also lacking the hooks of the shell muscle and muscle scar, as in the derived emarginuline genera *Lucapina* Pilsbry, 1890, and *Stromboli* Berry, 1954. The dominant shell sculpture would be radial, rather than the sharply clathrate and concentric sculpture of emarginuline and hemitomine genera. The derived emarginuline genus *Lucapinella* Pilsbry, 1890, has radial sculpture like that of *Fissurella*, and would be the logical connecting genus, if it had a fossil record.

The fissurelline radula is diagnosed as having an extremely narrow rachidian (McLean, 1984c). The rhomboidal rachidian of large-shelled species in the *Fissurellidea* group illustrated by McLean (1984b) is much broader than that of Fissurellinae, because it serves to separate the paired, large pluricuspid teeth positioned between the lateral and marginal teeth. However, within the Emarginulinae, narrow and elongate teeth of the central teeth are known in many of the small-shelled, deep-water genera of the *Fissurisepta* shell form reviewed by McLean & Geiger (1992: figs. 2G, 3G, 3L, 6G, 7D, 10G), which suggests that an understanding of transitional taxa between derived emarginulines and fissurellines should be sought in specimens that are small-shelled at maturity or small in juvenile stages. This may well show that distinctions between the subfamilies Emarginulinae, Hemitominae, and Fissurellinae are blurred during early ontogeny. There is a striking similarity between the mature radula of *Profundisepta profunda* (Jeffries, 1876) shown by McLean & Geiger (1998: fig. 3G) and the mature hemitomine radula illustrated here, because the narrow outer laterals of that species show a mid-shaft heel that calls to mind the transverse ridge of the hemitomine radula.

First Appearance of Fissurellid Subfamilies

Mazaev (1998) described a Paleozoic genus *Retchitsella* from the Upper Carboniferous of the Moscow Basin, based on a species of small size (2.2 mm) having clathrate sculpture and a high profile. He assigned *Retchitsella* to Emarginulinae, although there is neither a slit nor a selenizone. In the absence of these most diagnostic features of Fissurelloidea, that assignment has to be provisional.

Based on Warén & Bouchet (2005) and Knight et al. (1960), the earliest appearance of Fissurellidae Fleming, 1822, is Middle Triassic for *Emarginula* Lamarck, 1801, for the subfamily Emarginulinae Children, 1834. Sohl (1992) showed that *Diodora* was flourishing during the Late Cretaceous of the Caribbean; he also claimed that *Fissurella* was present because his species "*Fissurella*" *kollmanni* lacks the truncate interior callus ring of *Diodora*. However, because that species has clathrate sculpture like that of *Diodora*, I instead consider it evidence for a genus with an oval callus ring, comparable to *Stromboli*, a member of a generic group of derived emarginulines indicative of the transitional source group leading to fissurellines.

As detailed above, the Hemitominae Kuroda, Habe, & Oyama, 1971, are traced to *Loxotoma* Fischer, 1885, with a first appearance in the Upper Jurassic of Europe (Knight et al., 1960).

With the above mentioned correction of Sohl's Cretaceous record, the earliest member of the subfamily Fissurellinae Fleming, 1822, is still *Atractotrema* Cossmann, 1888, of the European Eocene (as in Knight et al. 1960). The better known genus *Fissurella* Bruguière, 1789, arose and radiated during the Oligocene of Europe.

The Molecular Phylogeny of Aktipis et al. (2011)

The recently published "five-gene molecular phylogeny" of selected genera of Fissurellidae by Aktipis et al. (2011) sequenced only five of the species here assigned to four different genera of the nine genera assigned to Hemitominae in my morphological analysis. Assigned to their concept of Hemitominae were *Hemitoma octoradiata* (type species of *Hemitoma*), and "*Hemitoma panhi*" (here assigned to *Montfortista*). Genera used by me for these species are considered to be in the derived group of hemitomine genera because the slit and selenizone are present only in the early juvenile stage. Species here treated as Hemitomine, but assigned to Emarginulinae by Aktipis et al. (2011) were *Emarginula variegata* and *E. foveolata fujitai* (both here assigned to new genus ***Variegemarginula***) and *Montfortula rugosa* (type species of *Montfortula*).

Genera recognized by me for these three species are considered basal in my definition of Hemitominae because they retain the slit and selenizone at all sizes. As could be expected, the first two species emerged as a sister group on their "maximum likelihood tree" (Aptikis et al., 2011: fig. 3) and the second three species formed another branch on the same tree. However, the first pair of their examined species emerged as sister to their only examined species of *Puncturella* and *Cranopsis* (genera regarded by McLean & Geiger, 1990 as within the emarginuline lineage). The second three species emerged on their Figure 3 between their species of true *Emarginula* and such other emarginuline genera as *Emarginella*, *Scutus*, and *Tugali*. This is a discrepancy in need of comment and possible explanation.

First, the observation that the length of the "*Hemitoma*" branch in the "maximum likelihood tree" (Fig. 3, of Aptikis et al., 2011) far exceeds the length of all other branches, which suggests the need for the inclusion of additional taxa of the genera regarded as derived in my morphological analysis.

A close look at tree B (Fig. 2B of Aptikis et al., 2011), the "strict consensus of all trees," indicates an unresolved polytomy of 16 branches, including 8 outgroups, all of which are subordinate to the pleurotomarioid outgroup. On this tree, my genera of Hemitominae appear twice, first, at the top, with the sister group *Hemitoma octoradiata/ Montfortista panhi* (regarded by me as derived hemitomines) preceding the rest of the outgroups, and again only as sister to *Puncturella/Cranopsis* standing alone in their analysis, preceding all the other species of Emarginulinae on their tree B. The last grouped emarginulines of their tree B are the type species of *Montfortula* and *Variegemarginula*, which are placed by me among the basal genera in my reinstated Hemitominae.

The improbability of connecting these two groups was noted by Aptikis et al. (2011: 250): "… the outer lateral radula and pluricuspid teeth differ between the genera, and *Hemitoma* lacks a visible shell fissure while *Puncturella* and *Cranopsis* have a fissure on the anterior slope. Furthermore, *Hemitoma* are generally found in a range of ocean depths from shallow water to 200 m, while *Puncturella* and *Cranopsis* are mainly deepwater organisms. Recovery of *Hemitoma* sister to *Puncturella* + *Cranopsis* was therefore an unexpected result of this analysis and warrants further investigation with increased species sampling from both genera. Nevertheless, results of this study suggest that a clade comprised of *Hemitoma*, *Puncturella* and *Cranopsis* could constitute a fourth subfamily of fissurellids, recognized here as Hemitominae Kuroda et al., 1971."

One correction to the above is that the redefined genus *Hemitoma* and other related genera occur in the intertidal and shallow sublittoral zones, chiefly in the tropics. It is more exacting to note that *Puncturella* and *Cranopsis* occur under cold conditions, submergent in deep water at tropical latitudes and in shallower water at higher latitudes.

I agree that their results do indeed need further investigation with increased sampling, but a connection of *Hemitoma* to *Puncturella* and *Cranopsis* can only be dismissed as highly unlikely. The polytomy indicated in their Figure 2B indicates that their molecular analysis is defective, so their definition of Hemitominae is rejected here.

The next molecular analysis should include the genera *Clypidina* and *Montfortulana*, which have what I am considering to be a derived state of the radula in my definition of Hemitominae.

Feeding Ecology

Hemitomine genera of the rocky intertidal (*Hemitoma*, *Clypidina*, *Montfortula*, *Montfortulana*) are easily mistaken for patellid or siphonariid limpets because the notch does not show in dorsal view. One hemitomine species (*Montfortula rugosa*) is known to feed on algae in the rocky intertidal of southern Australia (Creese, 1978), as mentioned in more detail under that genus. I have not found citations that treat the feeding in *Hemitoma* and *Clypidina*, but expect that similar feeding would be the case because of the close similarities in radular structure and because these genera also live in the exposed intertidal zone in which algal mats would be the obvious food source.

Feeding in the hemitomine genera is also is comparable to the feeding of *Fissurella* species of the subfamily Fissurellinae, in which algal feeding is known (Ward, 1966; Bretos, 1978; McLean, 1984c; Franz, 1990a, b).

Most genera of emarginuline fissurellids are more cryptic in offshore habitats and feed upon sponges or other sessile invertebrates. However, two of the basal hemitomine genera (***Hemimarginula*** n. gen., ***Variegemarginula*** n. gen.) occur in unexposed habitats in the rocky intertidal and at shallow depths.

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